

## NICHE SPECIFICITY OF TWO *GLYPHHELMINS* (TREMATODA) CONGENERS INFECTING *LEPTODACTYLUS CHAQUENSIS* (ANURA: LEPTODACTYLIDAE) FROM ARGENTINA

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**ABSTRACT:** Sixty-five specimens of the frog *Leptodactylus chaquensis* were infected by 2 *Glyphelmans* species (*Glyphelmans repandum*: 41%, and *Glyphelmans palmipedis*: 38%) in the small intestine. This study was designed to determine the site specificity of both species along the length of the small intestine by analyzing the distribution, niche overlap, morphological characteristics, and population dynamics. The location of *G. palmipedis* is very restricted, with the core infection site in the anterior small intestine. In contrast, *G. repandum* can be characterized as having an expanded niche within the small intestine. In single infections and with different intensities, individuals of both parasitic species showed preference for the anterior small intestine. In concurrent infections and with different intensities, the distribution of *G. palmipedis* did not change when *G. repandum* was present; however, displacement of *G. repandum* toward the middle of the small intestine was observed. *Glyphelmans* species used the same microhabitat and presumably the same food resource and were generally found to overlap more than expected by chance. This finding suggests the possibility of different feeding mechanisms given by differences in their pharynx size by 37%. Also, the coexistence of these could be associated with the differentiation of realized niches.

Several studies have argued that niche specificity of parasitic species is restricted by selective forces, such as reproductive efficiency, morphologic specialization (Rhode, 1994; Simková et al., 2006), and competition (Holmes, 1990; Friggens and Brown, 2005). These, and other observations (see Poulin and Morand, 2004), have also demonstrated that aspects of the host's biology, i.e., body size, diet, and behavior, and parasite's biology, i.e., site of infection, morphology, body size, and affinity, are responsible for determining the number of niches potentially available.

Niche specialization and the use of fragmented resources can be favored by the coexistence of potentially competing congeneric species (Simková et al., 2000). In another case, however, arguments exist as to whether species site selection and affinity are determined by competition. Esch et al. (1990) reviewed the literature regarding competition and indicated that this interaction can be considered in 1 of 3 ways. First, there is competitive exclusion, defined as the impossibility for 2 species with very similar requirements to coexist simultaneously in the same space. Competitive exclusion among helminth parasites has been best demonstrated in the experimental studies of Holmes (1973). Second, interactive site segregation involves segregation or specialization of niches by 2 species in which the realized niche of one, or both, is reduced by the presence of the other species (Holmes, 1973). Third, selective site segregation must be considered within an evolutionary context that has led the parasites to select narrow niches. In addition, Rohde (1979) has demonstrated that niche restriction can be an important factor for the reproductive activity of the parasites, because in the case of parasitic species that normally occur in low infrapopulation sizes, mating would be favored by a restricted distribution that would increase the opportunities for reproductive encounters.

To understand niche space, it is necessary to identify (1) the fundamental niche, i.e., the range of sites in which the parasite can develop, and (2) the realized niche, i.e., the optimal site within the fundamental niche if interaction with other species is unimportant, or the available site within the fundamental niche is due to antagonistic interaction with another parasitic species (Poulin, 1998, 2001).

During the course of a study on the ecology of parasites of amphibians, Hamann, Kehr, and González (2006) and Hamann, González, and Kehr (2006) reported that *Glyphelmans palmipedis* and *Glyphelmans repandum* commonly occur in leptodactylid frogs of South America. Both species are present within a reduced area of the small intestine. However, their study did not provide information regarding resources in terms of space, i.e., preferential site of infection within the small intestine of the frog, or time, i.e., preferential season, nor did it investigate whether these congeneric species differed in their realized niches. Based on certain assumptions, the approach employed in this current study predicts that (1) the distribution of 1 species in the intestine will shift in response to the presence of the second species, and vice versa, (2) closely related species or ecologically equivalent species will coexist in the same habitat and use the same nutrient resources via different morphological adaptations involving size and structure of the mouthparts, (3) the preference for different season may facilitate species coexistence, and (4) congeneric species commonly have widely overlapping niches. Therefore, the present study attempted to determine the site specificity of *G. palmipedis* and *G. repandum* along the length of the small intestine by analyzing the distribution, density, niche overlap, morphological characteristics, and population dynamics related to temporal variation of both species.

### MATERIALS AND METHODS

#### Study area

The study site is located in (27°27'S, 58°47'W). The area is mostly occupied by forest, with herbaceous strata formed by grasses, numerous cacti, and terrestrial bromeliads. Temporary, semi-permanent, and permanent ponds also occur in the study area.

#### Analytical procedure

Samples of *Leptodactylus chaquensis* were collected monthly during the winter of 2002 (n = 29 specimens), spring of 2002 (n = 43), summer of 2003 (n = 44), autumn of 2003 (n = 48), and winter of 2003 (n = 11). Sampling time was 4 hr for each collecting trip. Specimens were always collected by 2 people between 1900 and 2200 hr. Each sampling covered every possible microhabitat. Frogs were transported live to the laboratory and killed in a chloroform (CHCl<sub>3</sub>) solution; snout-vent length was measured. The hosts were sexed during necropsy, and their intestines were removed and examined. According to Goater and Goater (2001), the present study has complied with all the regulations and ethical and legal

considerations for the capture and use of animals established by the National Council of Scientific Research and Technical of Argentina.

The small intestine was divided into 3 (anterior, middle, and posterior) equal portions. Only 2 helminth species (*G. repandum* and *G. palmipedis*) were recovered from the small intestine of frogs. The specimens were observed in vivo, counted, and fixed with warm Raillet-Henry solution, then stained with carmine hydrochloride, cleared in creosote, and mounted in Canada balsam, for determining their specific status. Of the total worms found, 19 (*G. repandum*) and 20 (*G. palmipedis*) individuals, all adults, were measured (in  $\mu\text{m}$ ). Measurements were taken using an ocular micrometer and included the following morphometric variables: body length (BL), body width (BW), oral sucker length (OSL), oral sucker width (OSW), ventral sucker length (VSL), ventral sucker width (VSW), pharynx length (PHAL), pharynx width (PHAW), right testis length (RTL), left testis length (LTL), ovary length (OL), seminal receptacle length (SRL), and cirrus-sac length (CSL). Specimens were deposited in the Helminthological Collection of Centro de Ecología Aplicada del Litoral (Center of Applied Ecology of the Littoral), Argentina. Codes were used to indicate the seasons, as follows: 1, winter (21 June–20 September); 2, spring (21 September–20 December); 3, summer (21 December–20 March); and 4, autumn (21 March–20 June).

### Statistical analyses

Prevalence and intensity of infection were calculated as described in Bush et al. (1997). Communities of *Glypthelmins* spp. have been classified at the infrapopulation (all individuals of a *Glypthelmins* species within a single frog), infracommunity (all *Glypthelmins* infrapopulations within a single frog), and component community (all *Glypthelmins* infracommunities within a frog population) levels. Statistical analyses were made using Xlstat 7.5 software (Addinsoft, 2004). The spatial distributions were constructed to reflect the location of parasitic individuals in the small intestine of each host. The distribution of congeneric species in situations of low (1 individual) and high (more than 1 individual) intensities was used to evaluate possible interspecific interactions. Niche overlap of *Glypthelmins* species was calculated for each niche type at the infra- and component community levels using Pianka's index ( $O_{ij}$ ) (Pianka, 1973), which ranges from 0 (no shared infection sites) to 1.0 (identical infection site use). Overlap was calculated assuming equal availability of resources. To determine whether measured overlap values were significantly different from what would be expected based on random sampling of the species data, we performed a randomization analysis using EcoSim software (Gotelli and Entsminger, 2004). EcoSim performs Monte Carlo randomizations to create "pseudo-communities" (Pianka, 1986) and then statistically compares the patterns in these randomized communities with those from the real data matrix. In this analysis (randomization algorithms RA3: Winemiller and Pianka, 1990) reshuffled zero, all values of the original matrix were randomized 1,000 times, and niche breadth was retained for each species (Gotelli and Entsminger, 2004). The niche breadth for *Glypthelmins* species was calculated for each niche type using Levins's index (Levins, 1968) at the infrapopulation level. We also reported the standardized niche breadth by expressing it in a scale from 0 to 1 (Hurlbert, 1978). Aggregation was calculated using the measure of intraspecific ( $J$ ) and interspecific ( $C$ ) aggregation proposed by Morand et al. (1999):

Intraspecific aggregation:

$$J_1 = \left\{ \sum_{i=1}^p P_i [(n_{1i}(n_{1i} - 1))/m_1] - m_1 \right\} / m_1 \\ = [(V_1/m_1) - 1]/m_1,$$

where  $n_{1i}$ ,  $m_1$ , and  $V_1$  are the number in patch  $i$  (and  $p$  the number of patch), mean numbers, and the variance in number of species 1. A value of  $J = 0$  indicates that individuals are randomly distributed, whereas a value of  $J > 0$  indicates that parasites are aggregated compared to the random distribution.

Interspecific aggregation

$$C_{12} = \left\{ \sum_{i=1}^p P_i [(n_{1i}n_{2i})/(m_1P)] - m_2 \right\} / m_2 \\ = Cov_{12}/m_1m_2,$$

where  $Cov$  is the covariance between a pair of species. When  $C > 0$  the 2 species are positively associated, and when  $C < 0$  they are negatively associated.

The relative strength of intraspecific aggregation on interspecific aggregation was estimated using  $A_{12} = [(J_1 + 1)(J_2 + 1)] / (C_{12} + 1)^2$ . If  $A_{12} > 1$ , intraspecific aggregation is stronger than interspecific aggregation.

Principal component analysis (PCA) of previously standardized measurements (each variable: means = 0 and  $s^2 = 1$ ) was used to find the most significant meristic variable. To test the null hypothesis of no difference between metric variables, multivariate analysis of variance (MANOVA) was applied, including the more important components according to the PCA, previously transformed into natural logarithms (ln). Bonferroni's correction was used to identify significant ( $P < 0.006$ ) data in a univariate test (ANOVA).

## RESULTS

### Infrapopulation parameters

Sixty-five of the 102 *L. chaquensis* from Corrientes City were infected with *G. repandum* (prevalence = 41.0% [95% CI, 31.6–50.4%]; mean intensity =  $3.7 \pm 3.1$ ; intensity range: 1–11) and *G. palmipedis* (prevalence = 38.0% [95% CI, 28.6–47.4%]; mean intensity =  $2.1 \pm 1.7$ ; intensity range: 1–9) in the small intestine.

In the cases of single and concurrent species infection, the prevalence of *G. repandum* was 25% and 16%, and the mean intensity was  $3.0 \pm 2.6$  and  $4.8 \pm 3.6$  species per frog infected; the prevalence of *G. palmipedis* was 22% and 16%, and the mean intensity was  $2.3 \pm 1.8$  and  $1.8 \pm 1.4$  species per frog infected.

### Site specificity of parasites

*Glypthelmins repandum*: The great majority of worms were found in the anterior portion of the small intestine (125 of 154 worms), with only a few occurring in the mid-intestine. Similarly, occurrence of infection was highest in the same portion of intestine (76%). Niche breadth ranged between 1.0 and 1.6 for different infrapopulations, and standardized niche breadth varied between 0.0 and 0.6.

*Glypthelmins palmipedis*: The great majority of worms were found in the anterior portion of the small intestine (80 of 81 worms). Likewise, occurrence of infection was highest the same portion of intestine (98%). Niche breadth ranged between 1.0 and 1.2 for different infrapopulations, and standardized niche breadth varied between 0.0 and 0.2.

### Relationship between sites of parasite infection

Niche overlap between the proportion of *G. repandum* and *G. palmipedis* at the component community level was high ( $O_{ij} = 0.98$ ). Randomizations with all data produced a significant difference between measured (observed) overlaps and simulated (expected) overlaps using site infection ( $P$  [observed  $>$  = expected] = 0.0001). Consequently, the mean observed (0.98) was greater than the mean value expected by chance alone ( $0.63 \pm 0.37$ ). Similarly, niche overlap ( $O_{ij}$ ) at the infracommunity level showed high values, ranging from 0.95 to 1.00. This relationship was observed in the 62% of the cases where both species were together.

### Parasite intensity

In the cases of single-species infection, with different intensities, individuals of both parasite species showed preference for the anterior portion of the small intestine (Fig. 1). In cases of concurrent infection and with different intensities, the distribution of *G. palmipedis* specimens did not change with the presence of *G. repandum*, while the specimens of the latter species were

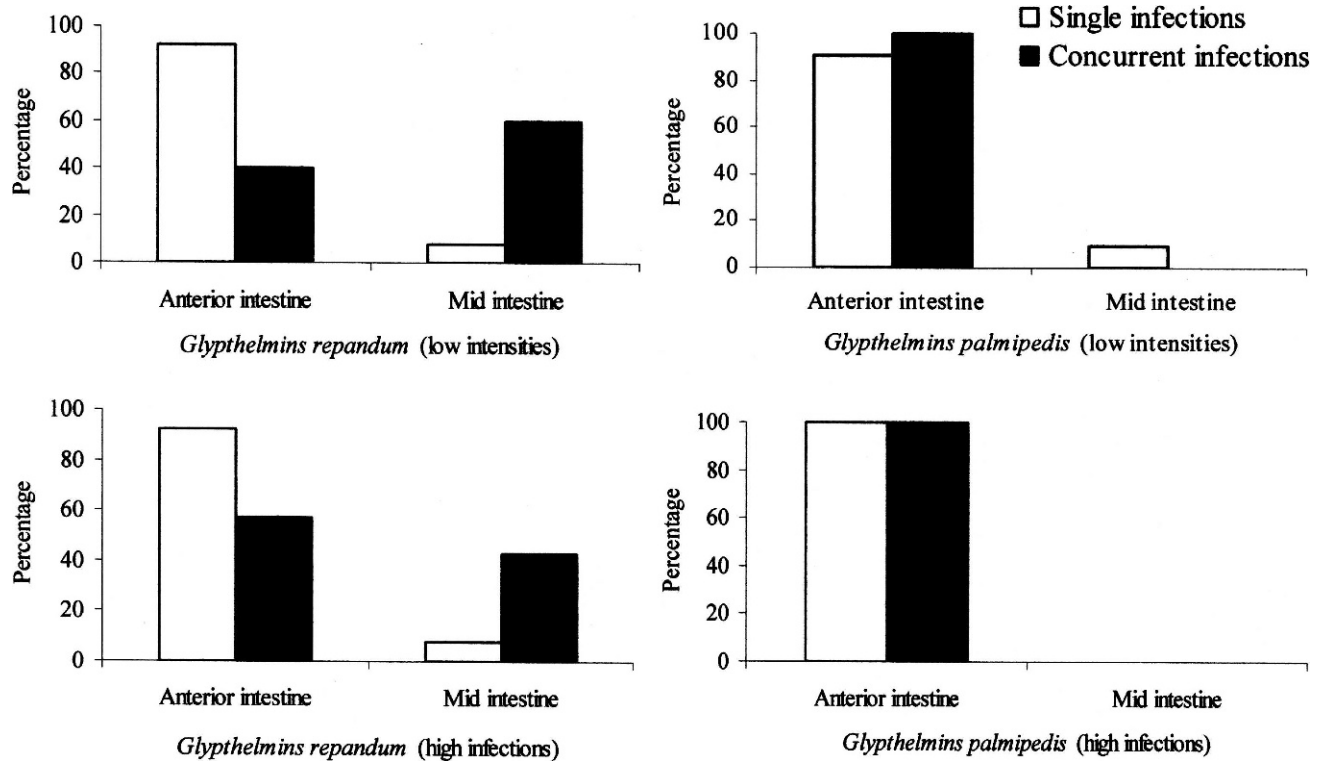


FIGURE 1. Percentage of distribution of 2 congeneric species (*Glypthelmins repandum* [n = 154] and *G. palmipedis* [n = 81]) of the small intestine (anterior and mid-portion) in situation of low (1 individual) and high (more than 1 individual) intensities, and in single and concurrent infections.

distributed more uniformly along the anterior and mid-portion of the small intestine.

The data of autumn 2003 with a similar mix of development stages in both species (Table I) were used to evaluate specifically whether the samples varying over time influence the identification of the niche specificity of the parasite. The present study demonstrates a very similar pattern of distribution by both *Glypthelmins* species along the small intestine (Fig. 2) with regard to the total heterogeneous samples tested (Fig. 1).

#### Parasite aggregation

In the anterior portion of the small intestine, both *Glypthelmins* species showed values of  $J > 0$  (*G. repandum*:  $J_1 = 3.19$ , *G. palmipedis*:  $J_2 = 1.92$ ), indicating that individuals of each species were aggregated at the infrapopulation level. This pair of species exhibited a value of  $C_{12} < 0$  ( $-0.07$ ), which indicates negative interspecific aggregation, and  $A_{12} > 1$  (14.14), verifying that intraspecific aggregation is greater than interspecific aggregation. Aggregation of *G. palmipedis* could not be calculated in the mid-portion of the small intestine because of low infection level (1 individual); for this sector, *G. repandum* showed  $J > 0$  ( $J_1 = 10.84$ ), which demonstrated aggregation of individuals at the infrapopulation level.

#### Correlation between morphometric variables

Table II shows the principal components and percentage of variance accounted for by the morphometric variables of individuals of *G. repandum* (n = 19 adult) and *G. palmipedis* (n = 20 adult). The first component reflected the influence of body length and width, ventral sucker length and width, and oral

sucker length and ovary length, while the second component was mostly affected by pharynx length and width.

A comparison of the 2 parasitic species showed significant difference in morphometric variables (MANOVA Wilks' Lambda = 0.06;  $F_{8, 30} = 56.05$ ;  $P = 0.0001$ ). Body length of *G. repandum* was significantly greater than that of *G. palmipedis* (ANOVA  $F_{1, 37} = 20.02$ ;  $P = 0.0001$ ). Sucker length was significantly greater in *G. repandum* compared to *G. palmipedis* (ANOVA  $F_{1, 37} = 21.39$ ;  $P = 0.0001$ ), and ventral sucker width of *G. repandum* was also significantly greater (ANOVA  $F_{1, 37} = 12.63$ ;  $P = 0.001$ ). Pharynx length of *G. repandum* was significantly smaller than that of *G. palmipedis* (ANOVA  $F_{1, 37} = 129.76$ ;  $P = 0.0001$ ), and pharynx width of *G. repandum* was also significantly smaller (ANOVA  $F_{1, 37} = 161.26$ ;  $P = 0.0001$ ).

#### Infection of parasites in relation to season

The data are incomplete, probably because of uneven monthly sample sizes of frogs; nonetheless, some seasonal trends are evident (Table I). The highest prevalence values for *G. repandum* were recorded in autumn; prevalence decreased gradually in winter, while mean intensity peaked in winter. The distribution of gravid parasites (stage II) peaked in summer (100%). Infections caused by non-gravid parasites (stage I) were highest in autumn (42%).

The infection parameters of *G. palmipedis* showed a different pattern. Prevalence increased gradually throughout the seasons, and mean intensity peaked in spring. The distribution of gravid parasites (stage II) peaked in spring (100%). Infections caused by non-gravid parasites (stage I) were highest in winter (50%).

TABLE I. Prevalence (%), mean intensity (MI) ± 1 SD, minimum and maximum intensity (range), total number of parasites (no.), and relative percentage of worms in stages per season (stage I–II) for *Glythelmins repandum* and *G. palmipedis* found in *Leptodactylus chaquensis* from Corrientes, Argentina.

	<i>Glythelmins repandum</i>					<i>Glythelmins palmipedis</i>					
	%	MI/SD	Range	Stage		%	MI/SD	Range	Stage		
				I	II				I	II	
Winter 2002	29	4.5/3.5	1–8	9	22	78	2.0/0.0	2–2	4	50	50
Spring 2002	43	3.2/2.8	1–10	29	7	93	5.5/2.7	2–9	22	0	100
Summer 2003	44	3.8/3.4	1–11	60	0	100	4.2/0.4	1–2	19	16	84
Autumn 2003	48	3.9/3.0	1–10	55	42	58	2.2/1.2	1–4	28	25	75
Winter 2003	11	—	1	1	0	100	1.6/0.8	1–3	8	36	63

**Relationship between seasonal infections**

There was high seasonal spatial overlap between the proportions of *G. repandum* and *G. palmipedis* individuals ( $O_{ij} = 0.94$ ). Randomizations using all data revealed no significant difference between measured (observed) overlaps and simulated (expected) overlaps using seasonal infections ( $P$  [observed <= expected] = 0.93, and  $P$  [observed >= expected] = 0.07). Thus, the overlap index observed (0.94) was high between the 2 species, but similar to that expected by chance ( $0.70 \pm 0.15$ ).

TABLE II. Results of a principal component analysis of morphometric variables of *Glythelmins repandum* (n = 19) and *G. palmipedis* (n = 20): Coefficients for standardized measurements and percentage of explained variation.

Coefficient	PC1	PC2	PC3
Body length	0.753	-0.384	-0.337
Body width	0.827	0.318	-0.096
Oral sucker length	0.780	0.520	-0.202
Ventral sucker length	0.847	-0.337	-0.290
Ventral sucker width	0.884	-0.236	-0.284
Pharynx length	0.121	0.955	0.120
Pharynx width	0.085	0.912	0.283
Ovary length	0.895	0.087	-0.010
Percentage of total variance explained	44.015	27.731	10.322
Cumulative percentage	44.015	71.746	82.068

**DISCUSSION**

Previous studies have shown that linked species commonly have widely overlapping niches, and that species with similar requirements cannot coexist in the same space; therefore, the coexistence of parasitic species has been studied in the context of niche restriction by specialization (Rohde, 1979, 1991; Simková et al., 2006) and interactive site segregation (Holmes, 1961, 1973, 1990; Patrick, 1991). In this sense it is assumed that interspecific interactions will exist between 2 species that belong to the same guild, i.e., absorbers, if they co-occur in the same niche within the host. For instance, Holmes (1961), in experimental infections, showed that interactive site segregation probably occurs in concurrent infection of the cestode, *Hymenolepis diminuta*, and the acanthocephalan, *Moniliformis dubius*, in the rat. When both

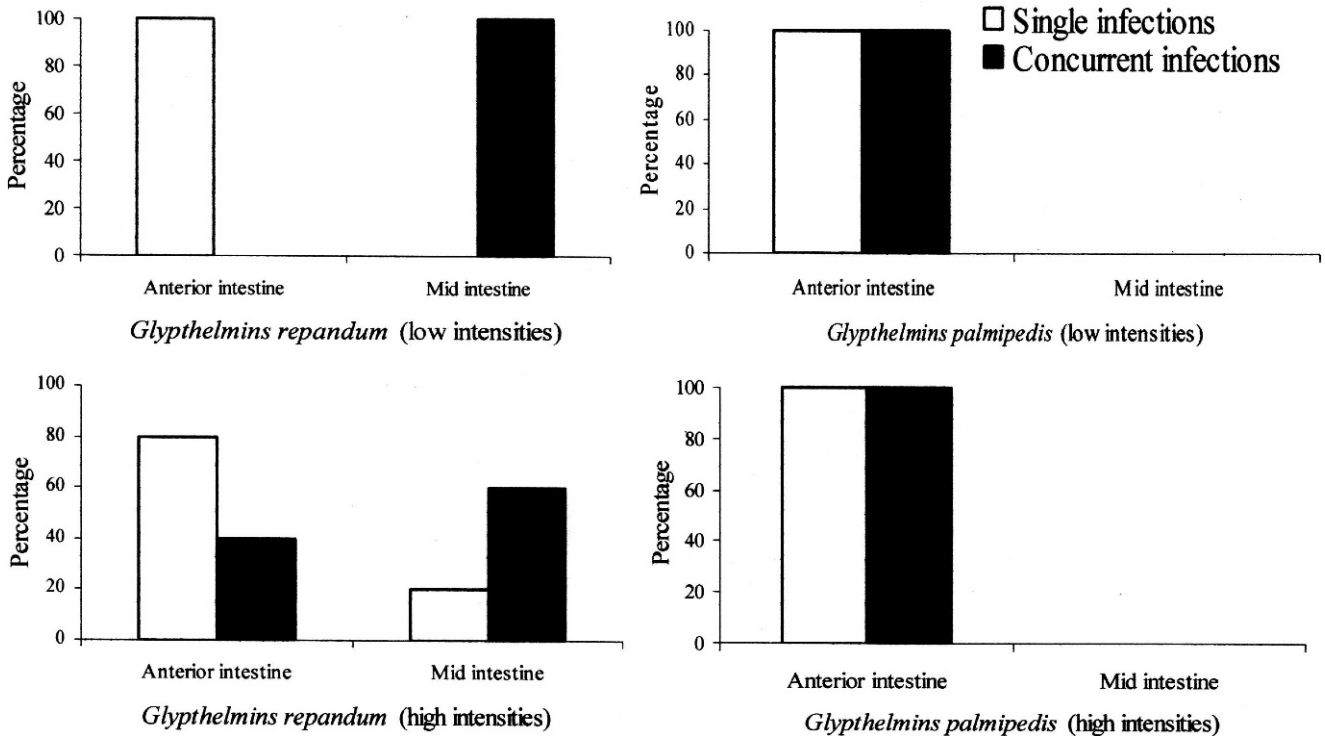


FIGURE 2. Percentage of distribution of 2 congeneric species (*Glythelmins repandum* [n = 55] and *G. palmipedis* [n = 28]) of the small intestine (anterior and mid-portion) in situation of low (1 individual) and high (more than 1 individual) intensities, and in single and concurrent infections.

helminths are together, the presence of 1 species typically causes a functional shift in resource use by the second species.

In the present study, a similar situation appears between both congeneric species in a natural infection. Thus, these species were found to inhabit mainly the anterior portion of the small intestine. *Glyphelmis palmipedis* has a very restricted location, with a core infection site in the anterior portion of the small intestine. In contrast, *G. repandum* alters its distribution and would generally be characterized by having an expanded niche, i.e., wide niche breadth, which favors its coexistence with *G. palmipedis*. This suggests that the coexistence of these species could generally be associated with the differentiation of realized niches. Additionally, these interactions clearly show no relation with potential ontogenetic migration (Fig. 2).

In contrast, specialization for exploitation of different resources is frequently achieved through morphological adaptation, quantified as a 10% minimum difference in linear measurements (see Holmes, 1973). Cannon (1972) showed that *Bunodera sacculata* and *Crepidostomum cooperi*, which co-occur in the anterior intestine of perch, have a 10% difference in oral sucker diameter. In this context, both *Glyphelmis* species have a 37% difference in pharynx size, suggesting the possibility of different feeding mechanisms that would allow these 2 species to feed on the same resource. These differences may reflect evolutionary niche shifts resulting from intense competition in the past (Holmes, 1973). In addition, the greater range of distribution of *G. repandum* indicates greater plasticity of this species' ecological requirements, which allows it to occupy less favorable zones in cases of co-occurrence with *G. palmipedis*, or at high intensities.

The analysis of the distribution of populations in single and concurrent infections at different intensities suggests the existence of other interspecific relationships that affect the distribution of *Glyphelmis* spp. in the intestine. In this sense, when both species coexist in an infracommunity, the distribution of *G. palmipedis* is constant, but *G. repandum* is displaced toward the mid-intestine, suggesting that morphological adaptation is not enough to avoid a certain degree of competition for food resources or the existence of density-dependent factors. Body size difference (20%) could also be a probable factor in the increased distribution range, mainly when the number of parasites increases at the infra-population level.

Parasites generally occur in aggregation (non-random distributions) within their host (Poulin, 1998). We found that parasites were aggregated at intra- and interspecific levels, and that intraspecific aggregation was stronger than interspecific aggregation. According to the Lotka-Volterra model, this relationship could favor unstable coexistence, avoiding competitive exclusion where both species can then coexist. Additionally, the negative and significant relationship between the abundances of both species seems to indicate that competition plays little actual role, or that the intensity of competition is reduced by intraspecific aggregation. Kennedy (1985) demonstrated that congeneric species of acanthocephalans can coexist without any clear evidence of interspecific competition; nevertheless, the possibility of such competition occurring in the future, or having occurred in the past, cannot be ruled out.

The life cycles of both *Glyphelmis* species have not been resolved, but it is likely they both have a 2-host life cycle involving a snail as intermediate host and *L. chaquensis* as the definitive host, which can live near the shore of temporary, semipermanent,

and permanent ponds and in flooded grass. Frog infection occurs via penetration of infective cercariae or by ingestion of infective metacercariae encysted in a tadpole or a young frog. Thus, this pattern is determined by adaptations of its complex life cycle to ensure transmission (Grabda-Kazubaska, 1976).

The distribution and seasonal changes of *G. repandum* and *G. palmipedis* appear to be complementary. These congeneric species infect the anterior intestine preferentially, but *G. repandum* in concurrent infections showed niche displacement, and both species showed peaks of infection in different seasons (temporal heterogeneity). Possibly, this differential seasonal production, e.g., intensity of infection, facilitates the coexistence of these congeneric species populations. Finally, both *Glyphelmis* species did not show a pronounced seasonal pattern of maturation, as observed by Hamann (2006) in an intensively study of seasonal biology of *G. vitellinophilum* in *Lysapsus limellus* from a subtropical permanent pond.

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